

MONARCHISTIC DOMINANCE IN SMALL GROUPS
OF CAPTIVE MALE MOSQUITOFISH,
GAMBUSIA AFFINIS PATRUELIS

MELBA C. CALDWELL¹ and DAVID K. CALDWELL²

Los Angeles County Museum

Dominance-subordinance interrelations among vertebrates have received considerable attention in recent years. Allee (1952) summarized the literature dealing with the more commonly reported of these, the peck-right or peck-dominance hierarchy, which has been described for all classes of recent vertebrates. A less frequently reported social order (also discussed, briefly, in the same paper by Allee) is that in which the despot not only dominates all of its associates, but also inhibits any interaction between the remaining members of the group. Collias (1944: 90) used the term "monarchistic" for this type of social organization.

Such a monarchistic dominance has been reported for captive male albino laboratory mice (Uhrich, 1938), for captive male domestic cats (Winslow, 1938), by Cooper (1942) for captive African lions (males over males and females), and possibly for captive male American chameleons (Evans, 1936). Allee (1952) mentioned that it is known to occur in fishes, but did not cite a specific species.

We now report the finding of monarchistic dominance behavior in captive male mosquitofish, *Gambusia affinis patruelis* Baird and Girard. Monarchistic was the usual dominance behavior demonstrated by the groups studied, in March and April, although one group of four fish for a time demonstrated a peck-right (or thrust-right) dominance of sorts in which three of the four interacted (the fourth neither chased nor was chased). This display of different types of dominance in mosquitofish is thus similar to the variations in types of social orders shown for the laboratory mouse (Uhrich, 1938). Although the fish were not actually measured, our notes indicate that in each of the dominance relations established during this study, the largest fish was the despot. This was true in the case of the American chameleons studied by Evans (1936), but was not true for the domestic cats reported on by Winslow (1938).

¹Also Department of Zoology, University of California, Los Angeles.

²Also Research Associate, Florida State Museum, and Collaborator in Ichthyology, Institute of Jamaica.

MATERIALS

Male *Gambusia affinis patruelis* were collected from a stream running through the botany garden on the University of California campus at Westwood Village, Los Angeles, California, and were identified using keys provided by Hubbs (1926).

PROCEDURE

Under varying conditions, up to four male *Gambusia* were integrated in a five-gallon aquarium and the water level reduced to one gallon, to reduce the area of confinement. Although in this series of observations there were many forms of aggressive behavior, possibly including some nipping or biting, thrust was taken as the most clear-cut demonstration. The thrust is usually directed at the victim's flank. Aside from thrust, preliminary dorsal fin erection forms a major part of the aggressive pattern.

Fighting, on the other hand, is carried out by the fishes making an "S" shape of their bodies and giving a sharp flip to the caudal fin. This propels a current of water against the opponent. On one occasion, two *Gambusia* fought continuously for 15 minutes using these "tail blows" (such as those described for other species of fishes by Tinbergen, 1958: 25), with intermittent thrusts at each other's flanks, before the dominant individual was established.

This dominant individual, or despot, roams freely throughout the tank. Once beaten, the subdued individual usually flees from the aggressor. Submission is indicated by holding quite still, or by swimming very slowly. The body is held parallel to the bottom of the tank. Fast swimming almost invariably brings on an attack by the despot. On occasion, a submissive individual will elude observation by the despot by sinking down into the aquarium where it seems to attract less attention.

Marking.—100 grams of Alizarin Red S dye were dissolved in 100 cc. of distilled water, and between 0.1 and 0.2 cc. were injected intramuscularly either in the caudal region, in the dorsal fin region, or both. This method allows for three separate markings and for one unmarked control.

In a series of 15 markings or remarkings, between April 12 and April 21, death was caused twice. Death was immediate, and mechanical marking injury was considered responsible. At no time was further ill effect noticed from this freshly-made solution. It should be noted that old Alizarin Red S solution is toxic to fish. On one occasion a solution 30 days old was used to mark eight males. Six died immediately

(apparently not from mechanical injury), one showed distress, and one showed no apparent ill effect.

Specimens retained their stain for varying lengths of time (two to seven days) and remarking did not interfere with the experiments.

RESULTS

Experiment 1 (13 March)

In a preliminary observation, definite aggression was shown by one of the larger males and in the space of one hour no interaction was noted between the other three. The aggressive individual thrust at the other three, who would flee from it. The aggressive actions by the despot were almost continuous.

Experiment 2 (21 March)

In this experiment the despot (which suppressed interaction between the remaining fish) was removed as soon as its dominance was established (in less than 30 minutes). There was an occasional interaction between submissive fish (three such interactions were noted in one hour), but this was rare once dominance was established. As the despot established himself, he was removed from the aquarium and placed in a container marked A. Interaction by the remaining three fish was begun almost immediately, and when another became dominant (after four to five minutes) he was transferred to a container marked B. Before his removal, he suppressed interaction between the remaining two fish. When one of these remaining two fish became dominant (after one to two minutes), he was placed in a container marked C. The fourth individual was placed in a container marked D.

Experiment 3 (11 April)

Four fish were starved for four days and then were integrated. A piece of shrimp was introduced and two of the fish carried out a 15-minute battle directly above the shrimp. During the fight, both of the other fish came under and fed. Once both fish stopped fighting to chase off a feeding fish, but immediately resumed their fight. After a dominant alpha individual was established, he curtailed interaction among the other individuals by (1) chasing any fast-moving fish in the aquarium—this could be either a chasing or a chased individual, or both, but his presence would stop the interaction, and (2) by juxtaposing his body (on two occasions) between an aggressor and his victim. In this latter instance, all three individuals held quite still.

Experiment 4 (12 April)

In this series of experiments, times of establishment of successive dominance were noted and the individuals were placed in separate tanks marked A, B, C, and D in their successive order of rank when the preceding despot was removed. The time required for A to become despot was not noted, but after his removal, B became despot in 10 minutes, and after his removal C became despot in four minutes. A was marked in the caudal region, B was left unmarked, C was marked in the region below the dorsal fin, and D was marked in both the caudal and dorsal regions.

Experiment 5 (12 April)

One hour after Experiment 4, the fish were integrated again and the same successive ranking manifested itself as each despot was removed. A was despot within ten minutes. After A was removed, B became dominant over C and D within four minutes, and after the removal of

TABLE 1

Number of thrusts in 30-minute periods in Dominance-Subordinance relationships of the mosquitofish, *Gambusia affinis patruelis*, after monarchial hierarchy established. *Upper*, four fish; *Middle*, after A removed, three fish remaining; *Lower*, after A and then B removed, two fish remaining.

(*Submissive individual on top of table, aggressive individual on side*)

	A	B	C	D
A	-	8	2	2
B	1	-	0	1
C	0	0	-	3
D	0	0	0	-

	B	C	D
B	-	11	8
C	0	-	0
D	0	0	-

	C	D
C	-	8
D	0	-

B, C, became dominant over D in four minutes. This was the same succession of monarchy as shown before marking.

Experiments 6 and 7 (13 and 14 April)

Experiment 4 was repeated twice within the next two days, with the same succession of monarchy resulting, using the same four individuals. In Experiment 6, the successive times in which the despot assumed his position were three, five and ten minutes. Times were not recorded in Experiment 7. In both of these experiments, the fish were well fed before they were integrated, after being kept in separate containers for nearly 24 hours.

During Experiments 6 and 7 the number of thrusts made by each individual was tabulated. Table 1 shows these data and clearly indicates that interactions among individuals below the despot were infrequent. It should be stated that they occurred early in the experiment, though this is not indicated in the table. In addition, thrust frequency is not very stable. Various factors seemed to influence the number of thrusts: (1) The existing despot varies as to degree of aggressiveness, and (2) The existing submissive individuals vary as to degree of submissiveness. If the submissive individual flees easily, he is harassed more than one that does not—as fleeing almost always stimulates chasing and thrusting. Also, if the submissive individual remains quiet, rather than moving around, he is usually ignored.

Experiment 8 (20 April)

In order to observe the effect of prior residence, B of Experiment 4 was placed in the aquarium and A was removed to a separate container for five days. Then A was returned to the aquarium. B thrust at A who did not flee, but could be edged around in a circle by B for the first ten minutes. For the second ten minutes, the fish usually avoided each other. Then A thrust at B twice within the next ten minutes, after which A became completely dominant. The pattern of A's thrusts at B after 50 minutes was as follows: Over a ten-minute period; five thrusts, rest, search, rest, six thrusts, rest, seven thrusts, rest, seven thrusts, rest, eight thrusts, rest, two thrusts, rest, five thrusts, rest. During this time, the submissive individual, B, would try to avoid contact if approached by the despot, A, or would hold very still. B fled quickly if thrust at.

Experiment 9 (21 April)

In the last experiment of this series, the effect of hunger on the dominance order of the fishes from Experiment 4 was studied. Indi-

viduals C and D were separated and starved for seven days. Individuals A and B, also separated, were well fed. The four fish were then integrated and food was introduced. For the first six minutes, D (the omega individual in the succession of monarchy) thrust, chased, and inflicted tail blows at A, B, and C. The following four minutes, C was dominant, engaging in the same aggressive actions against the other three fish. A then engaged B. During this period, C and D were intermittently feeding when not fighting. For a period of three hours and 20 minutes there was no continuing despot, and fighting occurred between all individuals. After this period, A reestablished himself as the alpha despot. Therefore, hunger, like prior residence, played a disrupting role in the dominance order, but did not have a permanent effect.

SUMMARY

There is definite dominance and subordination in small groups of captive male *Gambusia affinis patruelis* in which:

1. The dominance-subordination relationship is not affected by the marking methods employed during the study.
2. Usually, instead of a descending peck-order or thrust-order within a group, a single individual is dominant and represses aggression by other members of the group. This may be termed monarchistic dominance.
3. Within a short while after removal of a despot, a new despot manifests himself.
4. The order of succession of monarchy shows constancy over a period of time.
5. Dominance order is disrupted for a brief period of time by prior residence of a usually submissive individual, and for a much greater length of time by starvation of a usually submissive individual. In each case, the usually submissive individual becomes despot for a brief period.
6. A peck-right or thrust-right of sorts is sometimes demonstrated.

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